

Phosphorus fertilizer induced changes in the soil available P, the P nutrition and the growth of *Pinus radiata* seedlings grown in association with understory

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Received: 2009-09-10; Accepted: 2009-12-19

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Abstract: A study was carried out to investigate changes in the soil plant-available P, the P nutrition and the growth of *Pinus radiata* seedlings grown in association with understory, broom (*Cytisus scoparius* L.) or ryegrass (*Lolium multiflorum*) on Orthic Allophanic Soil, following the application of three rates of triple superphosphate (TSP) (0, 50, and 100 mg·kg⁻¹P) under a glasshouse condition. The application of P fertilizer enhanced P availability in the rhizospheric of radiata seedlings and the bulk soils in a P-deficient site. P availability in the rhizospheric soils of ryegrass and broom, grown in association with radiata, were also increased by the presence of radiata roots. P concentrations in new shoot needles, old shoot needles, stem and roots of radiata pine increased with increase rates of TSP application, but the effects of ryegrass and broom on P nutrition of radiata seedlings depended on the soil P status. In the absence of P fertilizer addition (control treatment), P concentrations in new shoot needles, old shoot needles, stem, and roots of radiata grown in association with broom were higher than those with ryegrass, whereas, when P fertilizer was added (50 and 100 mg·kg⁻¹) the P concentration was lower. This is probably related to the growth of broom that may have removed much of the plant-available P in the soil as indicated by the consistently lower Bray-2 P concentration in the rhizosphere soil of

radiata in association with broom than that in the rhizosphere soil of radiata in association with grass at the two high P rates. Furthermore, in the high P fertile soil (application rate of 100 mg·kg⁻¹), the dry matter yield of radiata was lower when it was grown with broom than with ryegrass. This result suggests that in moderate to high P fertile soils, *P. radiata* seedlings grow better with ryegrass than with broom, because broom grows vigorously in high P fertile soil and competes with *P. radiata* for P and perhaps for other nutrients as well.

Keywords: phosphorus fertilizer, *Pinus radiata*, understory, rhizosphere, soil available P, P nutrition, plant growth

Introduction

Phosphorus (P) fertilizer has been routinely applied to many areas of *Pinus radiata* (radiata tree) plantation in New Zealand, since the 1960's (Hunter et al. 1991, Payn et al. 1998, 2000), because most of the soils are P deficient or marginally deficient. Currently, radiata plantations in the country have been adopting silvicultural practices towards wider tree spacing and lower initial stocking, and also an increased rate of P fertilizer application (Payn et al. 2000). The wider initial tree spacing and lower initial stocking has increased the potential for weed growth in forest stands as light conditions below the canopy and nutrient resources are relatively better (Gadgil et al. 1988). A consequence of this is that the response of radiata trees to P fertilizer is expected to be more influenced by the interaction between the applied P fertilizer, the tree, and understory vegetation than the case in the past.

Many studies have shown that the presence of understory vegetation causes competition for nutrients, water, and light; hence, it reduces *P. radiata* growth and survival (Mead & Mansur 1993; Clinton et al. 1994; Watt et al. 2003). However, interaction between some understory species and *P. radiata* has been shown to provide beneficial effects to the trees. Richardson et al. (1996) reported that some species of grass, herbaceous broad-

Foundation project: This study was financially supported by Massey University and the Centre for Sustainable Forest Management at Forest Research Institute, New Zealand

The online version is available at <http://www.springerlink.com>

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Responsible editor: Chai Ruihai

leaves and buddleia have significantly increased P concentration in needles of 3-year-old radiata trees (synergism), but broom, gorse, lotus and pampas had no significant effect on needle P concentrations, when they were grown in a moderately fertile soil (Richardson et al. 1993). However, the effect of these plant species on soil available P was not reported.

Many of the experiments conducted to study plant interferences have not been very successful. This was partly due to inappropriate experimental designs employed. Some of the experiments failed to keep the soil weight (or volume) explored by the roots constant across all treatments (Snaydon 1991; Silvertown & Doust 1993; Freckleton & Watkinson 1999; Freckleton & Watkinson 2000). For example, Scott (2002) conducted a pot experiment in a glasshouse to study the effects of understory species (lucerne, *Medicago sativa* L. and ryegrass, *Lolium multiflorum*) on *P. radiata* growth, P uptake and soil P changes. He reported that there was an evidence of effects of interaction between radiata pine seedlings and lucerne on soil P dynamics. He also found that interaction effect of radiata seedlings and lucerne significantly increased P availability in the soil. However, issues to do with the experimental design make it difficult to draw firm conclusions from the work. The experimental design used by Scott (2002) had some problems. When the trees were grown alone in the centre compartment of a tray (containing 300 g soil), the tree roots, through the ectomycorrhizal hyphae, had access to nutrients and water in the additional 200 g of soil. Thus the soil weights explored by the roots of plants in the different treatments (radiata vs radiata + lucerne or radiata vs radiata + ryegrass) were different.

Furthermore, in some studies investigating the below-ground interference between plants, the above-ground interference was neither removed nor kept constant (Law & Watkinson 1987; Belcher et al. 1995; Twolan-Strutt & Keddy 1996; Freckleton & Watkinson 1999; Freckleton & Watkinson 2000).

Ryegrass and broom (*Cytisus scoparius* L.) are two of New Zealand's important weed species found in radiata pine plantations. In the plantations, ryegrass competes for the available soil moisture as well as nutrients (Mead et al. 1993; Mead & Mansur 1993; MacLaren 1993; Roy et al. 1998). Meanwhile, broom has escaped cultivation and has aggressively invaded not only radiata pine plantations but also other many natural areas. Their seedlings can out-compete radiata pine seedlings and retard reforestation in some sites (MacLaren 1993; Roy et al. 1998). In the present study, these two important weed species were chosen to be observed. Under current silvicultural practices of *P. radiata* plantations, a better understanding of the soil P chemistry, especially soil available P and P nutrition of radiata pine trees in association with understory plant species under different soil P levels is required. This information is useful for a better management of P fertilizer in the forest plantations. The objectives of this study were to investigate changes in the soil available P, the P nutrition and the growth of *P. radiata* seedlings grown in association with broom and ryegrass on Orthic Allophanic Soil, following the application of three rates of riple superphosphate (TSP) (0, 50, and 100 mg·kg⁻¹ P) under a glasshouse condition. Specific null hypotheses tested in the pre-

sent study were: (1) soil available P, radiata tree growth and the P nutrition will not be influenced by P fertilizer addition relative to a control treatment, and (2) no difference exists between radiata tree grown with broom and with ryegrass treatments in soil available P, radiata tree growth and the P nutrition.

Materials and methods

Experimental design and treatments

The trial was arranged in a split-plot design inside a glasshouse. The main-plot treatments were three rates of P fertilizer: 0, 50, and 100 mg·kg⁻¹ P (equivalent to 0, 50 and 100 kg·ha⁻¹ P, bulk density=1 g·cm⁻³, depth= 10 cm) applied as TSP (granules ground to pass through 250 µm; total P= 20.7%) to the soil. Each main-plot was split into four split-plots consisting of the following four plant combinations: (1) broom alone (compartment a), (2) radiata with ryegrass (compartment b), (3) ryegrass alone (compartment a), and (4) broom with radiata (compartment b). In each tray, compartment a and b were separated by nylon mesh (43 µm opening) to stop plant roots from one compartment getting into the other (Fig. 1).

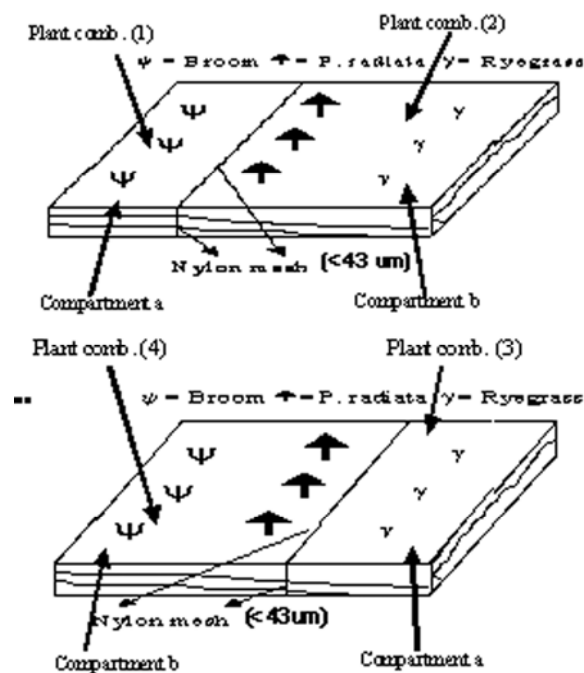


Fig. 1 Layout of the experiments with three P levels in the main plot and four plant combinations of radiata tree, broom and ryegrass in split plot

All treatments were replicated for five times. This study employed the divided pots design using below-ground partitions to get the expected root interferences (Pannell 1993); meanwhile the above-ground environment for all pots was homogeneous as the order of the plants in every pot was similar. The experiment was

designed in such a way to compare the effects of below-ground interaction of radiata + ryegrass and radiata + broom on the soil plant-available P, the P nutrition and the growth of radiata seedlings. The below-ground interference was studied in pots partitioned using nylon mesh (43 μ m opening) to stop plant rooting from one compartment to the other, but allow root interference between plants (radiata with ryegrass and radiata with broom) within the same compartment.

Bulk sample of soil collected from Kaweka forest, New Zealand (from a 0–10 cm depth) was used in this trial. This forest area had not received fertilizer for at least 30 years. The soil is classified as Orthic Allophanic Soil (Hewitt 1998, Soil Survey Staff 1999), with fine sandy loam texture, moderate medium crumb structure, non-sticky, non-plastic wet, and very friable moist.

To remove debris, the soil was air-dried and passed through a 5 mm sieve. A subsample of soil was ground to pass through a 2 mm sieve and analysed for chemical properties prior to planting.

Planting and maintenance of trial

Plastic trays used to grow the plants have rectangular shape, with internal dimensions of 245 mm wide, 307 mm long and 130 mm deep. Each tray (pot) was partitioned into two compartments, with 1/3 and 2/3 of tray volumes separated by a nylon mesh (with 43 μ m openings) which was sealed with glue to the edges and bottom of the trays. The nylon mesh was expected to stop entry of roots and most of the mycorrhizal hyphae from one compartment to the other. After 4.5 kg of air-dried soil (Water Content = 50%, equal to 2.25 kg oven-dried mass) was mixed homogeneously with the appropriate amounts of TSP, 1/3 and 2/3 of the soil was placed into compartment a and b, respectively in the trays (pots).

The seeds of radiata obtained from Forest Research Ltd., Rotorua were germinated according to the following procedure: soaked overnight, on December 10, 2001, in running tap water, planted in moist perlite in a box with a lid (box of 10 cm depth), and kept in a dark place at 22–24°C. All the seeds germinated in seven days. When the seeds were germinated, the box containing the seedlings was transferred to the glasshouse.

One week after germination, three radiata seedlings were transplanted into compartment b in each tray on December 26, 2001. At the same time, 10 broom seeds (from Forest Research Ltd.) were sown directly (after soaking 5 min in hot water at approximately 95°C) into compartment a or compartment b depending on the treatment and a week later the seedlings were thinned to four plants per tray. Four months later (April 9, 2002), ryegrass (variety Moata) seeds were sown and seven days after germination the seedlings were thinned to 10 plants per tray.

A complete but –P nutrient solution (Middleton & Toxopeus 1973) was added to all trays five months after the planting of the radiata seedlings. The nutrient solution was applied at a rate of 450 ml per tray four times during a two-week period, except the nitrogen stock solution which was applied only two times. Applications of nutrient solutions were made at 3–4 day interval. In total, each tray received 54.2 mg·kg⁻¹ N and 35 mg·kg⁻¹ K.

During growing period, the air temperature in glasshouse was maintained at 28°C maximum and 13°C minimum. Soil water content was maintained at 80% field capacity by bringing the weight of tray and soil to the required weight by adding distilled water (field capacity of Kaweka forest soil was 87% gravimetric water content). The weight of soil in each tray at 80% field capacity was 5.1 kg. Broom, ryegrass, and radiata were harvested on February 24, 2003 (56 weeks after planting broom and radiata; 42 weeks after planting ryegrass).

Soil sampling

Samples of the rhizospheric soil were collected according to the method of Adamo et al. (1995) and Wang and Zabowski (1998). The root-soil mass was shaken gently and the fallen soil mass was collected. This represented the bulk soil (bk), which was not influenced by roots. The soil closely adhering to the roots after the bulk soil had fallen away was collected by aggressively shaking the roots. This soil represented the rhizosphere (rh) soil. Each tray (pot) had four bulk soil and six rhizospheric soil sampling positions, which are referred to as:

1. bulk soil from broom alone (compartment a (B₁-bk))
2. rhizospheric soil from broom alone (compartment a (B₁-rh))
3. bulk soil from radiata grown with ryegrass (compartment b (R₂ + G₂-bk))
4. rhizospheric soil from radiata grown with ryegrass (compartment b (GR₂-rh))
5. rhizospheric soil from ryegrass grown with radiata (compartment b (RG₂-rh))
6. bulk soil from radiata grown with broom (compartment b (R₂ + B₂-bk))
7. rhizospheric soil from broom grown with radiata (compartment b (RB₂-rh))
8. rhizospheric soil from radiata grown with broom (compartment b (BR₂-rh))
9. bulk soil from grass alone (compartment a (G₁-bk))
10. rhizospheric soil from grass alone (compartment a (G₁-rh)).

All soil samples were passed through a 2 mm sieve to remove debris and stored at 4°C for measuring soil plant-available P (Bray-2P).

Plant sampling

Radiata and broom were harvested only at the end of the experiment at 56 weeks (February 24, 2003) after planting these seedlings. Ryegrass was harvested twice during the trial – firstly at 22 weeks (September 20, 2002), and secondly, at the end of the experiment at 42 weeks (February 24, 2003) after the ryegrass seeds were sown.

Shoots of radiata, broom and ryegrass were collected by cutting the plants approximately 1 cm above the soil surface. From the harvested radiata shoots, needle tips were collected by cutting the top 5 cm of the new growth in the seedlings (new shoot needles). Old shoot needles and stem were also retained. The stems and needles were dried in an oven at 70°C for 48 h and the dry

weights were recorded. After removing the rhizospheric soils as described above, the roots of all three plant species were washed free of soil and dried in an oven at 70°C for 48 h and the dry weights were recorded as well.

Chemical analysis

The soil pH was determined using a soil: water w/w ratio of 1:2.5. Soil suspensions were stirred and kept overnight at 20±2°C after which pH was determined using a pH meter equipped with a glass electrode (Blakemore et al. 1987). The organic matter content of the soils (expressed as percentage carbon) was determined by heating the samples in a stream of high purity oxygen in a Leco furnace to produce CO₂. The CO₂ was measured with an infrared detector (Leco Cooperation 1996) and the quantity of that gas used to determine the total organic carbon. Cation-exchange capacity (CEC) and exchangeable cations were determined by ammonium acetate leaching at pH 7 (Blakemore et al. 1987). The concentrations of K, Ca, Mg, and Na in the leachates were determined by atomic absorption spectrometry (AAS), and the ammonium concentration was determined using an Autoanalyser (Blakemore et al. 1987).

Phosphorus retention (an index of P fixation) was determined by measuring the P concentration in soil solution after 5 g soil was shaken with 25 ml solution containing 1000 µg·mL⁻¹ P for 16 h. Bray-2 P is the common soil test used for determining P availability in *P. radiata* plantation soils in New Zealand (Hunter & Hunter 1991; Giddens et al. 1997; Davis 2001). Bray-2 P was determined by shaking 2.5 g of air dried soil for one minute in 25 mL of a solution containing 0.3 mol·L⁻¹ NH₄F and 0.1 mol·L⁻¹ HCl and measuring the P concentration in the solution by the colorimetric technique of Murphy and Riley (1962) (Blakemore et al. 1987).

The dried needles, stem, shoot and root samples were ground using a hand-held Breve coffee grinder. The ground material was digested with a Kjeldahl digestion mixture containing 100 g of potassium sulphate and 1 g selenium powder in 1 L of concentrated sulphuric acid (95%–97%) (Twine and Williams 1971). Phosphorus concentrations in the digest were measured by using a Technicon auto-analyser (Searle 1975; Blackmore et al. 1987). The P uptake by radiata, broom and ryegrass was calculated by multiplying P concentrations in each plant part by the corresponding dry matter (DM) weight. The total P uptake by each plant species was the amount of P removed by all plant parts.

Statistical analysis

An analysis of variance (ANOVA) for a split-plot design was performed using SAS (SAS 2001). The least significant difference (LSD) test at $p < 0.05$, unless otherwise stated, was used to separate the means when the analysis of variance (ANOVA) results indicated that there were significant treatment effects (Steel et al. 1997). Data were square root transformed when the spread was proportional to the square root of mean and were log_e transformed when the spread was proportional to the treatment mean (Anon 2000; Steel et al. 1997).

Results

Soil available P

The plant-available P in the soil used in the study prior to planting in the glasshouse had very low Bray-2 P concentrations (approximately 3 mg·kg⁻¹P). In addition, it had very high fixation of phosphorus (92%) (Table 1).

Table 1. Chemical properties of the Orthic Allophanic Soil used in the study prior to planting in the glasshouse

pH (1:2.5 H ₂ O)	K (cmol _c ·kg ⁻¹)	Ca (cmol _c ·kg ⁻¹)	Mg (cmol _c ·kg ⁻¹)	Na (cmol _c ·kg ⁻¹)	CEC (cmol _c ·kg ⁻¹)
5.7	0.29	2.9	0.58	0.12	14
N (%)	P-total (mg·kg ⁻¹)	C (%)	P retention (%)	Bray-2 P (mg·kg ⁻¹)	
0.27	248	5.6	92	3	

The increase of the P fertilizer rate significantly ($p < 0.0001$) increased Bray-2 P concentrations, both in the rhizospheric and the bulk soils under all plant combinations (Table 2). The significant effect of P fertilizer rate on the Bray-2 P concentrations is not surprising as the soils without P addition had a low plant-available P concentration. Significant ($p < 0.0001$) differences in Bray-2 P concentrations between plant combinations were also observed. The interaction between P fertilizer rates and plant combinations was significant as well ($p = 0.0004$) (data not shown).

Table 2. Effect of the P fertilizer rate and plant combination on Bray-2 P concentration (µg·g⁻¹ soil) in the soil

Sampling position ¹	P fertilizer rate (mg·kg ⁻¹ P)		
	0	50	100
B ₁ -bk	2.9 ± 0.21bc ²	5.9 ± 0.25cd	7.8 ± 0.35d
B ₁ -rh	2.8 ± 0.13c	6.3 ± 0.05cd	7.9 ± 0.21d
R ₂ +G ₂ -bk	3.0 ± 0.15bc	6.5 ± 0.56bcd	9.5 ± 0.36bc
GR ₂ -rh	3.3 ± 0.15ab	8.2 ± 0.49a	11.3 ± 0.71a
RG ₂ -rh	3.0 ± 0.20bc	6.7 ± 0.09bc	9.6 ± 0.46bc
R ₂ +B ₂ -bk	3.0 ± 0.07bc	4.9 ± 0.16e	8.0 ± 0.32d
RB ₂ -rh	3.6 ± 0.06a	6.0 ± 0.33cd	9.1 ± 0.52cd
BR ₂ -rh	3.3 ± 0.41ab	7.3 ± 0.24ab	9.8 ± 0.73abc
G ₁ -bk	2.9 ± 0.21bc	5.6 ± 0.59de	9.6 ± 0.42bc
G ₁ -rh	3.0 ± 0.12bc	6.5 ± 0.25bcd	10.9 ± 0.34ab

Note: ¹B₁-bk: bulk soil from broom alone; B₁-rh: rhizosphere soil from broom alone; R₂+G₂-bk: bulk soil from radiata grown with grass; GR₂-rh: rhizosphere soil from radiata grown with grass; RG₂-rh: rhizosphere soil from grass grown with radiata; B₂+R₂-bk: bulk soil from broom grown with radiata; RB₂-rh: rhizosphere soil from broom grown with radiata; BR₂-rh: rhizosphere soil from radiata grown with broom; G₁-bk: bulk soil from grass alone; G₁-rh: rhizosphere soil from grass alone; ²Numbers under each P rate followed by the same letters are not different at $p < 0.05$; N = 5.

Plant P concentrations

The P concentrations were higher in new shoot needles than in old shoot needles, stem and roots (Table 3). The P concentration in new shoot needles for the 0 mg·kg⁻¹ P treatment was lower than 0.12%, which was commonly considered to be the deficiency threshold for 7 to 9-year old *P. radiata* trees (Mead & Will 1976; Will 1978). The P concentration in old shoot needles was, however, lower than this threshold for all P treatments. Phosphorus concentrations in new shoot needles, old shoot needles, stem and roots of radiata were significantly influenced by the rate of P fertilizer application ($p < 0.0001$, $p < 0.0001$, $p = 0.0016$, and $p = 0.0038$, respectively). The interaction of P fertilizer and plant combination on P concentration in all these plant organs was also significant ($p = 0.0145$ for new shoot needles, $p = 0.0105$ for old needles, $p = 0.0307$ for stem, and $p = 0.0369$ for roots) (data not shown).

Table 3. Effect of P fertilizer rate and plant combination interaction on P concentration (%) in radiata seedlings

Plant part	P fertilizer rate (mg·kg ⁻¹ P)		
	0	50	100
New shoot needles			
B / R + G ¹	0.109 ± 0.05aC ²	0.139 ± 0.06aB	0.181 ± 0.08aA
B + R / G	0.122 ± 0.05aB	0.125 ± 0.05bB	0.167 ± 0.07bA
Old shoot needles			
B / R + G	0.060 ± 0.005bC	0.088 ± 0.003aB	0.103 ± 0.003aA
B + R / G	0.074 ± 0.002aC	0.085 ± 0.002aB	0.103 ± 0.004aA
Stem ³			
B / R + G	0.038 ± 0.002 bB	0.045 ± 0.002aB	0.064 ± 0.005aA
B + R / G	0.048 ± 0.001aB	0.044 ± 0.002aB	0.062 ± 0.005aA
Root			
B / R + G	0.040 ± 0.002bB	0.046 ± 0.001aB	0.055 ± 0.002aA
B + R / G	0.051 ± 0.002aB	0.046 ± 0.002aB	0.056 ± 0.003aA

Note: ¹“/” represents nylon mesh separating the plants between compartment a and b in trays (see Fig. 1, B = broom, R = radiata, G = ryegrass); ²Numbers within the same column followed by the same lower case letters (plant combination) or within the same row followed by the same capital letters (P rate) for each plant part are not significantly different at $p < 0.05$; N = 5; ³Statistical analysis was performed on square root (\sqrt{Y}) transformed data

Dry matter yield

At the end of 56 weeks of radiata growth, there was a significant ($p < 0.0001$) response of radiata shoot, root and total (shoot + root) dry matter yield to P fertilizer rates. There was also significant ($p < 0.05$) interactions of P fertilizer rates and plant combinations on root and total dry matter yields but not on shoot dry matter yield.

Shoot, root, and total radiata dry matter yield increased markedly with the additions of 50 and 100 mg·kg⁻¹P compared with the control treatment (Table 4). There was however no significant difference in any of these yields between 50 and 100 mg·kg⁻¹P treatments.

Discussion and conclusions

Soil available P

The Bray-2 P concentrations in this soil was still lower than the critical P concentration of 12 mg·kg⁻¹P reported for radiata seedlings (Ballard 1974), even with application of TSP at a rate equivalent to 100 kg·ha⁻¹ P. This is due to the high fixation of P by this Orthic Allophanic Soil (Clark & McBride 1984; Parfitt 1989), hence, it is likely that most of the fertilizer-P added had been converted into less available soil P fractions.

Table 4. Effect of TSP fertilizer rates and plant combinations on shoot, root and total dry matter weights (g·pot⁻¹) of radiata seedlings after 56 weeks of radiata growth in the Orthic Allophanic Soil in the glasshouse

Plant part	P fertilizer rate (mg·kg ⁻¹ P)		
	0	50	100
P rate main effect			
Shoot	10.5 ± 1.2B ¹	62.6 ± 2.7A	66.0 ± 3.8A
Root ²	2.6 ± 0.3B	18.0 ± 1.3A	20.0 ± 3.3A
Total ³	13.1 ± 1.6B	80.6 ± 3.5A	86.0 ± 5.2A
P rate x plant combination			
Shoot	(lsd ($p < 0.05$) = ns)		
B / R + G ⁴	9.9 ± 1.3	62.6 ± 2.5	72.6 ± 2.0
B + R / G	11.1 ± 1.1	62.5 ± 3.0	59.3 ± 4.6
Root ²			
B / R + G	2.3 ± 0.2aB	17.2 ± 1.1aA	23.6 ± 1.5aA
B + R / G	2.9 ± 0.3aB	18.8 ± 1.5aA	16.4 ± 2.2bA
Total ³			
B / R + G	12.2 ± 1.6aB	79.8 ± 3.1aA	96.3 ± 3.2aA
B + R / G	14.0 ± 1.5aB	81.4 ± 3.9aA	75.6 ± 7.3bA

Note: ¹Numbers within the same row followed by the same capital letters (P rate) or within the same column followed by the same lower case letters (plant combination) for each plant part are not significantly different at $p < 0.05$; N = 5; ²Statistical analysis was performed on loge (Y) transformed data; ³Statistical analysis was performed on square root (\sqrt{Y}) transformed data; ⁴“/” represents nylon mesh separating the plants between compartments a and b in trays (see Fig. 1, B = broom, R = radiata, G = ryegrass)

Phosphorus fertilizer application enhanced P availability in the rhizosphere and the bulk soils of radiata seedlings in a P-deficient Allophanic Soil. The P availability in the rhizosphere of grass and broom, grown in association with radiata, were also increased by the presence of radiata roots. In general, the Bray-2 P concentrations in the rhizospheric soil of radiata was higher than that in the rhizospheric soils of the associated plants (GR₂-rh > RG₂-rh and BR₂-rh > RB₂-rh). This indicates that radiata can help to increase soil P availability to the associated plants in high P-fixing, P-deficient soils. This is consistent with the finding by other studies where there were increases in inorganic P, Olsen P and Bray P following land-use change from grassland to pine plantation (Chen et al. 2000; Scott 2002; Chen

et al. 2003).

Furthermore, for each of the P rates, especially at the rates of 50 and 100 mg·kg⁻¹P, the Bray-2 P concentration in rhizospheric soils of radiata was higher than that in the bulk soil regardless of the associated plant (GR₂-rh > R₂ + G₂-bk and BR₂-rh > R₂ + B₂-bk). This is probably related to organic anions (especially oxalate) released by radiata roots, which would have mobilized P in the rhizosphere (DeLucia et al. 1997). In addition, this could also be due to the lower pH of radiata rhizosphere soil. Increase of P availability following a decrease in soil pH has been reported by Hedley et al. (1982a) in a study with rape fertilized with KH₂PO₄ (Hedley et al. 1982b). They explained that the increased P availability with a decrease in rhizosphere pH was due to an enhancement of P dissolution from acid-soluble forms of soil P_i. Still another reason for the increased Bray-2 P concentration in the radiata rhizosphere is the higher phosphatase activity in the radiata rhizosphere (Liu et al. 2004), which could have increased the rate of mineralisation of organic P, resulting in a higher concentration of labile inorganic P.

Table 5. Phosphorus uptake by radiata, broom and ryegrass (mg·pot⁻¹) for each P rate and plant combination

P rate	Plant combination (μg·g ⁻¹ P)	Plant species		
		Radiata (R)	Broom (B)	Ryegrass (G)
0	B / R + G1	6.7 ± 0.5b ²	3.0 ± 0.2c	2.8 ± 0.1b
	B + R / G	9.3 ± 0.5b	5.2 ± 0.2c	1.0 ± 0.1b
50	B / R + G	54.2 ± 0.7a	8.7 ± 0.4bc	4.2 ± 0.3a
	B + R / G	52.8 ± 1.0a	11.5 ± 0.3b	3.1 ± 0.2ab
100	B / R + G	78.3 ± 1.3a	16.9 ± 0.3b	5.5 ± 0.2a
	B + R / G	61.9 ± 1.6a	34.7 ± 0.7a	4.7 ± 0.3a

Note: ¹“/” represents nylon mesh separating the plants between compartments a and b in trays (see Fig. 1); ²Numbers within the same column followed by the letters are not significantly different at $p < 0.05$; N = 5

The Bray-2 P concentration in the rhizospheric soil of radiata in association with broom (BR₂-rh) was consistently lower than that in the rhizospheric soil of radiata in association with ryegrass (GR₂-rh) for the P rates of 50 and 100 mg·kg⁻¹P. This is, probably, due to higher P uptake by broom than ryegrass (Table 5), causing a higher depletion of Bray-2 P concentrations in the soil.

Plant P concentration

Increased P fertilizer rates significantly increased P concentration in new shoot needles, old shoot needles, stem and roots of radiata pine trees regardless of the plant association (Table 3). This is consistent with the effect of P rates on plant available P concentration in the soil reported earlier (Table 2). Liu et al. (2004) also reported increased P concentration in different parts of shoots of seedlings grown on soil taken from the same forest plantation with increased rates of P application.

When no P was added, P concentrations in new shoot needles, old shoot needles, stems and roots of radiata were higher (most cases significant at $p < 0.05$, but all cases significant at $p < 0.1$)

when radiata was grown with broom compared to that with ryegrass. When P was added (50 and 100 mg·kg⁻¹P), however, the P concentration in these plant organs were significantly lower or not different when radiata was grown with broom compared to radiata grown with ryegrass. Higher shoot needle P concentrations in the presence of broom at zero P application could be due to broom supplying more available N to radiata through N-fixation (Gadgil et al. 1984; Beets & Madgwick 1987; Li et al. 2003a; Watt et al. 2003). The higher N availability to radiata might have helped radiata to take-up more P from the soil (Gillespie & Pope 1989; Li et al. 2003b).

When P was added (50 and 100 mg·kg⁻¹P) broom removed a higher proportion of the plant-available P from the soil and this may have caused a significantly lower P concentration in the new shoot needles of radiata in the presence of broom, compared to that in the presence of ryegrass at these rates of P application. Such a decrease was not observed in old shoot needles, stem, and roots. This lower P concentration in the new shoot needles when radiata was grown with broom was consistent with the Bray-2 P concentration in the rhizospheric soil of radiata in association with broom (7.3–9.8 mg·kg⁻¹P), which was lower than with ryegrass (8.2–11.3 mg·kg⁻¹P) (Table 2), indicating a higher depletion of soil plant-available P due to the higher P uptake by broom than by ryegrass (Table 5).

In conclusion, the P concentration in new shoot needles, old shoot needles, stem, and roots of radiata increased with increased rates of triple superphosphate application rate to a P-deficient Orthic Allophanic Soil, but the effects of ryegrass and broom on P nutrition of radiata seedlings depended on the soil P status. In the absence of P fertilizer addition (control treatment), P concentration in new shoot needles of radiata grown in association with broom was higher than that of radiata grown with ryegrass. However, when P fertilizer was added (50 and 100 mg·kg⁻¹P) the new shoot needle P concentration was significantly lower when radiata was grown with broom than that with grass.

Dry matter yield

The highly significant effects of P fertilizer rate on these dry matter weights are not surprising as the native soil had a very low plant-available P concentration (Table 2). These results are consistent with the increase of P concentration in both new and old shoot needles with the increased rates of P application (Table 3).

The interaction effects of P fertilizer rate and plant combination on total dry matter and root dry matter were demonstrated by the significant difference in these yields at the P fertilizer rate of 100 mg·kg⁻¹P between radiata grown with broom and radiata grown with ryegrass, but not at the P fertilizer rates of 0 and 50 mg·kg⁻¹P (Table 4).

The needle P concentrations in new shoots were significantly lower (0.167%) when radiata was in association with broom than with ryegrass (0.181%) at the P rate of 100 mg·kg⁻¹P (Table 3). This suggests that there was competition between broom and radiata for P at this high rate of P application, as indicated by a higher P uptake by both plants at the P rate of 100 mg·kg⁻¹P

compared to that of 0 and 50 mg·kg⁻¹P (Table 5). It is also possible that there was competition for N between broom and radiata even though broom was fixing atmospheric N. The N-fixed was probably not sufficient to meet the N needs of the vigorously growing broom. Using ¹⁵N isotopic studies, Watt et al. (2003c) also reported that there was competition for N when broom was grown with radiata in a forest located near Hororata, Christchurch.

Furthermore, Scott (2002) compared the dry matter yield of radiata seedlings, radiata seedlings grown with lucerne (a legume like broom), radiata seedlings grown with ryegrass, lucerne grown alone, and ryegrass grown alone in pots containing Immature Pallic Soils having different soil fertility levels with respect to total P and organic carbon. The results suggested that there might have been competition for P between radiata and lucerne when they were grown together in the high P fertility soil.

The present experiment revealed that in a high P fertile soil (application rate of 100 mg·kg⁻¹P), the dry matter yield of radiata was lower when it was grown with broom than with ryegrass. This result suggests that in moderate to high P fertile soils, *P. radiata* seedlings grow better with ryegrass than with broom, because broom grows vigorously in high P soil and competes with *P. radiata* for P and perhaps for other nutrients as well.

Acknowledgements

The authors thank the Massey University and the Centre for Sustainable Forest Management at Forest Research Institute, New Zealand for funding of the research. Suggestions on the manuscript by P Loganathan and A Arvanza Rivaie; and laboratory assistance by Arvina Utami, Bob Toes, and Ross Wallace of Massey University are also gratefully acknowledged.

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